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Measuring Decomposition, Nutrient Turnover, and Stores in Plant Litter

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Decomposition processes represent a major flux of both fixed carbon (C) and nutrients in most terrestrial ecosystems, and quantifying rates of litter mass loss and the concomitant changes in nutrients bound in the litter are important aspects of evaluating ecosystem function. Plant litter decomposition plays an important role in determining carbon and nutrient accumulation, as well as the rate and timing of nutrient release in forms available for uptake by plants and soil biota. Litter decomposition and nutrient dynamics are controlled to varying degrees by substrate quality (litter morphology and chemistry), abiotic conditions (temperature, moisture, soil texture), and biotic activity (microbial and faunal; Kurcheva 1960; Heath et al. 1964; Bunnell et al. 1977; Bunnell and Tate 1977; Parton et al. 1987). Thus, decomposition processes can serve as "integrating variables" for evaluating ecosystem function, for comparing different ecosystems, and for evaluating management practices or other anthropogenic influences (Coleman and Crossley 1996).

Decomposition involves not only mass loss but also changes in the nutrient content of plant litter and the eventual release of nutrients therefrom. Decomposition involves leaching of soluble organic and inorganic components, catabolic breakdown of organic matter, and comminution or physical fragmentation of litter (Swift et al. 1979). These processes ultimately transform senescent plant material into both labile and stable organic matter both above- and belowground. Methods used for quantifying rates of mass loss often can be used to determine changes in nutrient content as well. The dynamics of nutrients in decomposing litter can be complex, and decomposing litter can alternately act as either a nutrient sink or a source. This varies as a function of the nutrient under consideration, litter quality, biotic activity, exogenous nutrient inputs, and stage of decomposition.

In addition to quantifying rates of mass loss and nutrient dynamics of decomposing litter, it is often desirable to quantify the stores, or standing stocks, of various plant litter pools. Standing stocks of both coarse (i.e., woody) and fine (i.e., leaves, fine roots, etc.) plant litter represent important carbon and nutrient reservoirs in terrestrial ecosystems. The sizes of these reservoirs are influenced by both rates of litter production and decomposition, and are sensitive to changes in either process. Unfortunately, there are relatively few large-scale direct measurements of plant litter stores, and regional, national, and global estimates of these pools are often modeled based on input and decomposition rate data (e.g., Birdsey 1992; Harmon and Chen 1992; Kurz et al. 1992; Turner et al. 1995).

Our understanding of, and ability to model, litter decomposition, soil organic matter formation, and the storage of carbon and nutrients in ecosystems will be much improved if researchers design decomposition experiments and conduct inventories that lend themselves to broader synthesis. Our goals in this chapter are to present standard protocols for quantifying decomposition dynamics and standing stocks of most pools of plant litter. Two important exceptions are soil organic matter and very fine roots (<0.5 mm diameter), which are best studied using methods described in Chapter 5, this volume, and Chapter 20, this volume, respectively. Because methodologies vary for different types of plant litter, our discussion is divided into seven sections.

Available Methods

Fine Litter Decomposition

Many methods have been used to determine rates of fine plant litter decomposition. All have problems, and they serve mainly as indices of decomposition rates. Although we recommend only the litterbag method, we discuss other methods as potential alternatives. In the litterbag method preweighed material is confined within mesh bags and changes in mass, nutrient content, and carbon chemistry are measured over time (Falconer et al. 1933; Lunt 1933, 1935; Gustafson 1943; Bocock and Gilbert 1957; Bocock et al. 1960; Gosz et al. 1973). This method excludes macroinvertebrates, which are important elements of the decomposer community in many ecosystems. The litterbag can also alter the microclimate within the bag by slowing drying rates (Witkamp and Olson 1963) and can reduce rates of fungal hyphal colonization and growth (St. John 1980).

Time-series methods analogous to litterbags are (1) litter baskets that confine materials between a fine mesh bottom and a coarser mesh hardware-cloth top to allow access to macroinvertebrates (Stevenson and Dindal 1981; Blair et al. 1991) and (2) tethers to connect litter material while leaving it completely exposed (Witkamp and Olson 1963; Lang 1974). These methods also have problems. In the case of litter baskets, the potential input of additional material in situ may restrict their interpretation to areas with relatively large leaves (e.g., broadleaf forests). Tethered material, while exposed to invertebrates and natural microclimatological conditions, is subject to high rates of physical fragmentation, which can overestimate decomposition.

A chronosequence approach, in which annual accumulation layers are separated and analyzed for changes in mass, nutrient content, particle size, and type has also been used (Kendrick 1959). This approach (i.e., a substitution of space for time) can yield extremely interesting information. However, there must be clear indicators to mark the annual layers, and one must assume annual rates of litterfall are constant and that mixing of the layers is minimal.

There are several indirect methods for measuring decomposition, including harvesting litter plots, comparing paired plots, and calculating input-output balances. In areas with discrete periods of litterfall, decomposition rates can be calculated by comparing the lowest and highest stores of litter (Tyler 1971; Loomis 1975) or by measuring seasonal changes in stores (Capstick 1962; Weary and Merriam 1978). The paired plot method has had limited success; the concept is to remove inputs from two similar plots, harvest the litter at time zero in one plot and after some period in the second plot (Singh and Gupta 1977). The problems are that the paired plots often differ in the initial stores of litter, and preventing additional litter inputs is very difficult. The best-known indirect method is to calculate decomposition rate constants from litter-input:standing-crop ratios (Olson 1963). This method has been widely used, but it may give incorrect values if the standing stock is not in steady state or if the inputs are not completely accounted for (e.g., fine root inputs) or if the standing stock is difficult to measure.

We have selected the litterbag method as the standard protocol for determining the rate at which fine litter decomposes and accumulates or releases nutrients. Although the method has limitations, it is highly repeatable, relatively inexpensive, and widely used. Several types of litterbag systems have been used in the past, most differing in the size of the mesh used to contain the litter. We recommend a range of sizes depending on the purpose of the study. We strongly recommend that studies be conducted well beyond the traditional time length of 1–2 years as the carbon and nutrient dynamics of the early decomposition stages are relatively well known compared with the transition period from litter to stable soil organic matter (Lousier and Parkinson 1978; Berg et al. 1984; Edmonds 1984; Aber et al. 1990).

Woody Detritus Decomposition

Several methods are available to determine rates at which woody detritus decomposes, forms soil organic matter, and accumulates or releases nutrients. Harmon and Sexton (1996) provide a thorough review of these methods, including their relative merits.

Two frequently used approaches are (1) chronosequences that give a short-term snapshot of processes and (2) a time-series approach that is a long-term effort yielding excellent resolution of temporal patterns and processes. In the chronosequence approach, one ages as many pieces of detritus as possible in various states of decay and examines how a parameter such as density changes through time. Dates can be taken from fall scars, seedlings, living stumps, and records of disturbance (e.g., fire, insect outbreak, windstorm, thinning). This approach has been used extensively for coarse woody detritus (e.g., Graham 1982; Grier 1978; Harmon et al. 1987; Means et al. 1987; Sollins et al. 1987) and also can be used for downed fine woody detri-

tus (Erickson et al. 1985) and dead coarse roots (Fahey et al. 1988). The interpretation of chronosequence data varies depending on its use, typically either the conversion of volume measurements into mass or nutrient stores (see later) or the determination the rate mass is lost or nutrients are accumulated or released. If the aim is to use a decay chronosequence to estimate rates of mass loss or nutrient release, then the data must be adjusted for past fragmentation losses to estimate these rates correctly (Harmon and Sexton 1996).

Although chronosequences produce results quickly, there are serious temporal resolution problems caused by errors in dating and estimates of initial conditions. A time series circumvents these problems by examining how a cohort of pieces progresses through time, thereby avoiding the substitution of space for time. Although the method requires substantial investments in effort and time, it lends itself nicely to process studies. In addition to examining a chronosequence of pieces, one can also indirectly estimate decomposition rates of woody detritus from a chronosequence of different-aged stands (e.g., Gore and William 1986; Spies et al. 1988) by assuming each stand-creating disturbance left a similar amount of material. In many cases this assumption is not justified and can lead to significant uncertainty concerning decomposition rates. Finally, the ratio of input to stores can be used to indirectly estimate decomposition rate constants of woody detritus (Sollins 1982). This is subject to the same errors as for fine litter, compounded by the fact that both inputs and stores of woody detritus are highly variable.

Given the greater precision and site specificity of the time-series approach, we recommend this method to study the decomposition and nutrient dynamics of woody detritus above- and belowground. We recommend the chronosequence method to determine the density, carbon content, and nutrient concentrations of decay classes used to estimate mass and nutrient stores.

Standard Substrate Decomposition

Standard substrates can be used to determine the effect of environment on decomposition (Jenney et al. 1949; Tsarik 1975; Piene and Van Cleve 1978). Although these materials are somewhat artificial, they can provide an index of micro- and macroenvironmental controls on decomposition. Standard substrates low in nitrogen (N) (e.g., cellulose and wood) can indicate local variations in nitrogen availability (Binkley 1984). Standard substrates can be natural litter such as wheat straw, which is low in nitrogen and moderate in lignin content, or artificial substrates such as cellulose pulp or filter paper, cotton cloth strips, various small pieces of wood (including Popsicle sticks and chopsticks), and wooden dowels and blocks.

Our standard protocol uses two substrates: cellulose filter paper and hardwood dowels. We have selected these because they are commonly available and are low in nitrogen, and thus sensitive to nitrogen availability.

Organic Horizon Stores

The most common method to determine stores in organic horizons is to harvest material within a small plot. Plot size has varied from as large as 1 m $\times$ 1 m (Grier and

Logan 1977) to the more common 10–30 cm squares (Metz 1954; Youngberg 1966; Federer 1984). Steel corers 3–12 cm in diameter have also been used, but in cases where organic horizons are sparse this methodology is difficult to apply. Other methods, such as recording the depth of organic horizons and converting to mass with a measured bulk density, may be suitable for deep layers such as peat, but for most other situations the variation in bulk density is too high for reliable mass determinations. Therefore, the fuel survey methodology (Brown 1974) is not recommended as a standard protocol.

Our recommended method is to harvest organic horizons within a small square template with the approximate dimensions of 25 × 25 cm. Use of larger templates or corers has not been demonstrated to decrease the variability between samples (Capstick 1962). A better strategy is to use a greater number of smaller samples to reduce variability, which can be considerable (Weary and Merriam 1978; Carter and Lowe 1986).

Fine Woody Detritus Stores

Several alternative methods exist for measuring fine woody detritus stores (Harmon and Sexton 1996). The most straightforward is harvesting and weighing material within small plots (<4 m^2). Downed fine woody detritus can also be estimated using planar transects in which the number of pieces in size classes is recorded and then converted to stores using the mean diameter and bulk density of the size class. Unfortunately, the latter two parameters are rarely measured or reported (see Harmon and Sexton 1996 for available data); therefore, stores estimated by this method have questionable accuracy. Moreover, although the planar transect estimates the volume of downed, surface wood, it does not measure other important forms of fine woody detritus including dead branches or dead coarse roots. By using fixed-area plots the same methods can be used on all forms of woody detritus. This allows a better aggregation of these pools into a total woody detritus store that will integrate more closely with the methods used to estimate live tree mass, the source of woody detritus. Fixed-area plot sampling also has advantages for long-term measurement because the area in which trees are dying matches that of the woody detritus sample.

We recommend weighing downed branches in fixed-area plots for determining fine woody detritus stores. Dead branch and coarse root stores have rarely been estimated, and we recommend using an allometric approach based on the basal diameter of downed logs, stumps, and standing dead trees that is adjusted for decay state.

Coarse Woody Detritus Stores

For coarse woody detritus (>10 cm diameter and >1 m long) it is impractical to remove and weigh pieces. Therefore, for downed logs, standing dead trees, and stumps it is more usual to record piece dimensions within fixed-area plots (Harmon et al. 1987) or along planar transects (Warren and Olsen 1964; Van Wagner 1968; Brown 1974) to estimate volume, which is then converted to mass and nutrient stores using decay class–specific bulk density and nutrient concentration values. We strongly

discourage visual estimates from photographic comparisons (Maxwell and Ward 1976a, 1976b; Ottmar et al. 1990) because this method can be very inaccurate.

We recommend that fixed-area plots be used for determining woody detritus stores. Although the planar transect is a good, fast method, it does not measure standing dead trees or stumps. Because these two types of woody detritus often form major pools, a methodology that can be used for all types of woody detritus is preferable. By using fixed-area plots one can use the same methods on all forms of woody detritus and can sample them on the same area. This has the advantages for aggregation and long-term measurements discussed earlier under fine woody detritus stores.

Fine Litter Decomposition

The recommended protocol for examining fine litter decomposition, nutrient release, and formation of stable soil organic matter is to use the litterbag method in a time series. This method may be used for fine roots, leaves, twigs, reproductive parts (including cones), and small bark fragments. Because much less is known about mass loss and changes in litter chemistry during later stages of decay (Aber and Melillo 1980, 1982; Berg et al. 1984; Melillo et al. 1989), we suggest designing decomposition studies to last more than 5 years.

Materials

The materials needed to construct, place, and retrieve litterbags include:

1. A suitable quantity of air-dried litter
2. Litterbags (see procedures, below, for construction guidelines)
3. Nylon thread or Monel staples to seal the litterbag
4. Tags, either aluminum or plastic
5. Flagging to mark location
6. Shovel for burying belowground litterbags
7. Heavy nylon monofilament or braided nylon line to tether litterbags
8. Plastic bags to transport and store retrieved litterbags
9. High-quality paper bags to dry litter
10. Drying oven with a 50–55 °C range

Procedure

1. Litter selection. Decomposition data are most useful when the materials studied span a wide range of litter quality (LIDET 1995; Trofymow 1995). The simplest indicators of litter quality are C:nutrient ratios, most often C:N ratios (Singh and Gupta 1977). However, lignin:N ratios (Melillo et al. 1982), the relative concentrations of lignin and cellulose (ligno-cellulose index, or LCI, as defined by Aber et al. 1990), soluble phenolic content (Palm and Sanchez 1990), and phosporus and calcium contents are also useful indicators of litter quality.

2. Litterbag construction. Litterbags should be made of relatively nondegradable, inert materials. Mesh size can have a major effect on the invertebrate community consuming the litter, the microclimate, and the degree of fragmentation (Heath et al. 1964), and will depend on study objectives and environment. For aboveground placement, 1 mm nylon mesh has often been used and in low-light environments can last several decades. For environments with high levels of UV radiation (i.e., deserts, grassland, harvested forest areas), we recommend using fiberglass mesh (1.5 mm). For extremely small litter (e.g., *Larix* needles), we recommend woven polypropylene swimming pool cover or shade cloth (0.4 mm), a material extremely resistant to UV degradation. To allow access to macro- and megafauna, mesh must be at least 2 mm (see Chapter 7, this volume). Litterbags can be constructed to have the same material on the top and bottom or can have a larger mesh on the top than the bottom. The latter design prevents the loss of small fragments during long-term incubations. The smaller-mesh bottom can be made of Dacron sailcloth (50 μm) in low light environments or woven polypropylene in high UV environments. For belowground placement, litterbags can be constructed of Dacron sailcloth on both sides because UV degradation is not a consideration. Litterbags should be 20 cm × 20 cm and sewn and double-stitched on three sides using nylon thread (polyester thread is sensitive to UV degradation). Bags made of polypropylene can be heat-sealed effectively. Litterbags should be identified with unique numbers embossed on small aluminum or plastic tags that can be attached using UV-resistant cable ties. We also recommend placing a subset of litterbags partially filled with an inert polymer such as polyester fiberfill to estimate the mass and characterize the chemistry of materials transported into litterbags during the course of field incubation.
3. Litter collection. Although leaf litter is the tissue type most commonly used in decomposition studies, inclusion of root and fine woody materials such as twigs is of particular value, since they often represent large inputs to soils (Vogt et al. 1986). If the intent is to mimic natural litterfall, leaves should be collected from senescent plants in the case of herbaceous species or from branches ready to shed leaves in the case of woody plants. In the latter case it is often possible to "strip" leaves off branches. If this is not possible, then placing a clean drop cloth beneath the tree or branch and shaking will cause leaves to fall. In situations where live plant residues are a major source of litter (e.g., an agricultural field or a harvested forest), cutting green material may be appropriate. Regardless of the method used to gather litter, it is essential to report the source when presenting results.

We recommend that fine roots be excavated from a site similar to where they eventually will be placed. An alternative is to use roots from ingrowth experiments. One may also grow plants in controlled nutrient conditions and harvest the roots. This method has the advantage of allowing one to label roots with isotopes to enhance the interpretation of decomposition and nutrient dynamics. Finally, one can use fine roots from tree seedlings grown in nurseries that are being either discarded or trimmed prior to storage. Given that the substrate quality may vary with the source, even for a single species, it is essen-

tial that lignin, nitrogen, and other measures of substrate quality be determined.

4. Filling litterbags. Litter materials should be air-dried for at least 1 week prior to filling bags. Ideally, each bag should initially contain 10 g (air-dried) material because this leaves a sufficient amount for chemical analysis even after extensive decomposition. Subsamples of each litter should be set aside for oven drying at 55 °C and subsequent chemical analyses. We recommend placing the litter on a pre-tared pan and then placing the litter inside the bag after it has been weighed. Litterbags can be sealed in several ways: (1) by sewing the bag shut with thread, (2) by sealing with Monel staples (a nonreactive alloy) using five to six staples per 20 cm length of bag, or (3) heat sealing if the bag is made of polypropylene. It is important to record any losses from fragmentation during transport. One can use a set of "traveler" bags, which are taken to the field site, handled as the other litterbags, and then retrieved after placement. Reweighing these bags determines the average losses caused by transport and handling.
5. Initial chemistry and moisture content. When filling litterbags, 10 g samples should be periodically taken to determine the moisture content and initial chemistry of the litter. If the material has been properly air-dried, the variation in moisture will be quite small (+/− 1%). If weather conditions change radically over the course of filling the litterbags, it is important to take moisture samples frequently. These moisture samples should be weighed prior to and after oven drying to a constant mass to calculate dry weight conversion factors (air-dry mass:oven-dry mass) for each litter type used. Multiplying the dry-weight conversion factor by the air-dry mass will give the estimated oven-dry mass of each sample. Oven-dried material should be stored in sealed containers for future chemical analysis in a cool, dry environment. We strongly recommend a total mass of 50–100 g be set aside for these purposes.
6. Sampling interval. Uniform recommendations of sampling intervals are difficult to make due to climatic variability among regions. However, because mass loss and both carbon and nutrient dynamics change most rapidly during the early stages of decay, sampling intervals should be geometric. If the intent is to determine early leaching and very labile carbon losses, then a sample 1–4 weeks after placement may be necessary. Otherwise samples should be collected for three seasons (spring, summer, fall) in arctic and temperate ecosystems for the first year, and at 1–2 month intervals for moist tropical ecosystems. After the first year, we suggest increasing sampling intervals to once or twice per year in arctic and temperate ecosystems and 3–6 months in tropical systems.
7. Litterbag placement. It is important to avoid pseudoreplication (Hurlbert 1984). Separate sets of litterbags should be placed either in replicated units (ecosystem types, experimental plots, etc.) or in single plot types located along documented environmental gradients (e.g., fertility, moisture, temperature, or elevation gradients). Sufficient numbers of samples should be set out to allow for retrieving at least four to five litterbags per litter type used per plot at each sampling time.

Normally, litterbags should be placed in locations where the litter type under investigation is most likely to enter the soil system. Leaf and fine woody litter samples should be placed at the surface of the litter layer, whereas fine root material should be inserted into the profile where they normally grow and die. We recommend that above ground litterbags be pinned to the surface to limit movement. The recommended procedure for placing litterbags below ground is to push a shovel into the soil at a 45° angle, prying the resultant slit open until there is enough space to slide the litterbag all the way in, and then extracting the shovel. Good soil contact can then be established by gently tamping the raised portion of the soil.

To aid retrieval it is best to tether sets of litterbags to lines (either heavy-gauge monofilament or braided fishing line) that are flagged at both ends. If more than one litter type is tethered to a single line, samples should be placed in random sequence along the line. Each line should be sufficiently long (typically 5–10 m) to encompass variations in microhabitat at the site. Prepare a sketch map indicating the location of the litterbag "lines" with respect to permanent landmarks.

8. Litterbag retrieval. Utmost care should be taken to ensure that decomposing litter materials do not fragment and fall out of litterbags during retrieval or prior to processing. Litterbags should be cleaned of adhering particles (soil, mosses, rock fragments, etc.) to the extent possible in the field and placed individually into plastic bags immediately after being collected. Samples can be refrigerated for up to 1 week before processing, but if processing is delayed for more than a week, samples should be stored frozen.
9. Sample processing. Several options may be used to process litterbags. In cases where samples are not contaminated with large amounts of sand or soil, process the moist samples by carefully brushing the surface of the litterbag, cutting it open, and carefully turning it inside out onto a clean sheet of paper or into a large tray. If decomposition has been extensive, the inside of the litterbag can be scraped with a spatula to remove adhering particles of organic matter. Any living plant parts (e.g., roots or moss) as well as extraneous matter such as rocks and large soil particles should be removed. Do not remove decomposed organic matter or invertebrate feces (frass) from the litter, as these materials could be derived from the original material. Instead, use organic matter accumulation in unfilled litterbags to estimate the possible contribution of exogenous organic matter to the sample. The fresh weight of the material should then be determined and the sample placed in a paper bag, dried at 55 °C until the mass is stable, and then weighed to determine the dry weight.

When sand or fine soil contamination is high, obvious extraneous matter should be removed. Then oven dry the sample and finally sieve it to remove the bulk of the sand or finer soil. Because it is often difficult to remove all this material, a subsample of the contaminating soil should be retained to determine the carbon and nutrient content so that litter concentrations can be corrected.

After sample dry weights have been recorded and checked, grind each sam-

ple separately to pass a no. 40 sieve and store the dried, ground samples in sealed glass or polypropylene containers until they are analyzed for chemical constituents (see Chapter 8, this volume). Additional sample preparation and grinding may be required depending on the types of analyses that are planned.

Calculations

Samples obtained from litterbags in contact with the mineral soil often contain a mixture of the decomposing original litter and some soil from the surrounding area. Therefore, litter dry weights need to be corrected for soil contamination before determining mass loss or calculating decomposition rate constants. Often a subsample of the ground litter is ashed for 4 hours at 450 °C, and the mass remaining is expressed based on the percent ash-free dry mass (AFDM) of the initial and final litter samples. This is appropriate when soils are very low in organic matter but is not satisfactory for soils with a relatively high organic matter content, since the organic matter of the soil will contribute to the apparent organic matter mass of the litter. Instead, we recommend the use of the following soil correction equation (Blair 1988a):

$$FLi = (SaAFDM - SlAFDM)/(LiAFDM - SlAFDM)$$

where

FLi = the proportion of litterbag sample mass that is actually litter
SaAFDM = the percent AFDM of the entire litterbag sample
SlAFDM = the percent AFDM of the soil from which the litterbag was retrieved
LiAFDM = the percent AFDM of the initial litter

The underlying assumptions of this equation are that the organic matter content (percent AFDM) of the litter remains constant during decomposition, and that organic matter content of the contaminating soil can be determined. The equation then calculates the proportion of litter and soil that must have been mixed to produce the measured percent AFDM of the entire litterbag sample. The weight of the litterbag sample can then be multiplied by the correction factor (*FLi*) to obtain the weight of the litter remaining. In soils low in carbonates, the same correction can be applied by using percent carbon in place of percent AFDM. For soils high in carbonates, the concentration of these substances will have to be determined before a correction can be made.

The accumulation of soil in the litterbags also affects apparent nutrient concentrations in the litter. Therefore, the nutrient concentrations of litterbag samples contaminated with soil (as indicated by reductions in percent AFDM) should be corrected using the following equation (Blair 1988b):

$$LiNt = [SaNt - (FSl \times SlNt)]/FLi$$

where

LiNt = the nutrient concentration in the residual litter

SaNt = the nutrient concentration of the entire litterbag sample
FSl = the proportion of the litterbag sample mass that is actually soil (1 − *FLi*)
SlNt = the nutrient concentration of the soil
FLi = the proportion of the litterbag sample mass that is litter (from the above soil correction equation)

Special Considerations

The litterbag approach has limitations that need to be considered. In ecosystems where macroinvertebrates play a major role in decomposing litter, the small mesh sizes proposed here will exclude these organisms and thus underestimate decomposition rates. In this case it may be best to use multiple mesh sizes (see Fig. 17.1 in Chapter 17, this volume). For buried litterbags, the high amounts of residual material typically formed (McClaugherty et al. 1984) may be caused by the artificial environment. In particular, the fact that root litter is separate and not intermingled with the soil may alter the decomposition process (Fahey et al. 1988). The proposed protocol thus precludes studying the effect of soil texture and structure on physically protecting litter and incipient soil organic matter. If the latter is of interest, then incorporation of soil of known characteristics into the root litterbags as they are filled may be the method of choice. Finally, the recommended correction for soil contamination can be problematic for species with high ash contents. To test the underlying assumption that ratio of ash to dry mass for litter remains constant over decomposition, plot AFDM versus the cumulative mass loss from a location where soil contamination is minimal.

Fine Woody Detritus Decomposition

Fine woody detritus takes several forms, including attached and downed dead branches and coarse roots (>1 cm). The methods described in this section are appropriate for all these forms of detritus, regardless of whether the material is suspended off the ground, lying on the soil surface, or within the soil. For small pieces (<1 m long and <10 cm diameter), an approach analogous to the litterbag method can be used, weighing entire pieces before and after a period of incubation. Because of their size and structural integrity, however, woody samples do not need to be confined.

Materials

The materials and equipment required to conduct decomposition and nutrient studies for fine woody detritus include the following:

1. A source of branches or coarse roots
2. Chainsaw to cut large wood pieces
3. Miter saw, hand saws, and clippers to cut small wood pieces
4. Calipers (0–150 mm range) to measure thicknesses of samples
5. Diameter tape to measure piece circumference

6. Tape measure or ruler to measure piece length
7. Aluminum tags to mark samples
8. UV-resistant cable ties to attach tags to pieces
9. Plastic bags to carry samples (1–120 L depending on piece size)
10. Paper bags for drying samples (no. 2 to no. 10 depending on piece size)
11. Portable electronic scale if work is conducted at remote site
12. Electronic scales with ranges of 0–1500 g and 0–6000 g depending on piece size
13. 1 mm nylon mesh to cover buried pieces
14. Nylon braided cord to tether pieces

Procedure

1. Sample interval. As with fine litter, the standardization of intervals between sampling times is not recommended given the dependence of decomposition rates on substrate size, quality, and site conditions. We suggest the sample interval should be approximately 10% of the expected maximum life span. The number of times samples are collected will be study-dependent, but five sample times are recommended as a minimum.
2. Species selection. Species selection for a time-series experiment depends on the degree of species richness and the number of functional classes present in a location. Except for large, diverse genera with resistant heartwood such as *Pinus* or *Quercus,* little precision is gained by sampling below the genus level. The minimal suggested design is to select common species that represent the fast and slow ends of the decay resistance spectrum. This has the advantage of allowing one to compare the range of decomposition rates among sites. If additional resources exist, species with intermediate or extremely high decay resistance should be included.
3. Substrate quality descriptors. Physical variables are more commonly used to describe differences in woody substrates than in fine litter, in part because differences in substrate chemistry are less variable in wood than are chemistry differences in leaves, fine roots, and other small plant parts (Harmon et al. 1986). We recommend that at a minimum the total diameter, length, radial thickness of the major tissue types (i.e., outer bark, inner bark, sapwood, and heartwood), the total volume, and bark cover be measured. Because bark, sapwood, and heartwood decay at different rates, it is crucial to know their proportions. This allows one to understand why sizes and species decompose at different rates and to adjust results based on the proportions of these tissues. In addition to these physical descriptors, measurement of the same chemical descriptors used for fine litter is important.
4. Size selection. Since the decomposition of wood is in part a function of size, it is crucial that size differences be considered. We recommend that a range of diameters be used at each site so that statistical adjustments for size effects can be made. A geometric series of diameters is probably most useful, since the effect of diameter tends to decrease with size (e.g., 1, 2, 4, 8, 15 cm). A tolerance of 20% should be allowed for variation in diameter (other-

wise too many pieces will be rejected). When assigning pieces to size classes, also record the diameter of each piece to use as an independent variable. For intersite comparisons, species or sites can be compared directly where classes overlap, or indirectly by comparing regression slopes of decay rate on size, or by adjusting for size effects.

5. Collection of materials. Unlike fine litter, it is often difficult to find woody material that has recently senesced. A more likely source of material will be recently fallen trees from windstorms, or to fell trees using a chainsaw. To collect coarse roots, examine sites of recent road or house construction for access to recently excavated stumps. As materials for fine woody detritus are collected, we suggest cutting pieces at least 2.5 times the final length because this will greatly reduce the number of moisture samples required to estimate the initial oven-dry weight (see later).
6. Sample preparation. For small pieces of branches and coarse roots, one should determine the initial mass by weighing the entire sample. In addition, the diameter at the midpoint and the total length should be measured on each piece. If one is careful to cut lengths uniformly, a subsample of lengths can be measured. However, it is crucial to measure the diameter of each piece. Because one should not oven dry pieces before they are placed in the field, it is necessary to estimate the initial moisture content. This parameter is highly variable and should be determined for each piece. By cutting material in the initial field phase at least 2.5 times the final length, one can generate two pieces for each moisture sample taken. Either a miter or a radial arm saw can be used to prepare branch or coarse root samples. First trim off the ends that have been exposed to drying for more than a few hours. Then remove a thin piece for moisture determination, cut the first sample length, remove another sample for moisture content, cut the next sample length, and so forth, until the remaining piece is too short to be used. Use a uniquely numbered aluminum tag and a UV-resistant cable tie to identify each piece to be placed in the field. Bags containing the moisture content (labeled with individual piece numbers that they correspond to) should be dried at 55 °C until the weight is stable. Use the ratio of oven-dry weight to fresh weight to estimate the initial moisture content of individual sample pieces. Subsamples of this material should be saved for determining the initial chemical composition and ash content of samples. Extra pieces and odd lengths of material should be saved to determine the thickness of the tissue layers comprising samples of various sizes. At a minimum we suggest that bark and wood thickness be recorded, but one should also note the presence of zones high in resins (i.e., knotlike material), which are particularly decay-resistant. Finally, the source of the material should be noted because branch, bole, and coarse root material can differ substantially in their initial density, bark thickness, and chemistry.
7. Sample length. The length of pieces used in fine woody detritus time-series decomposition studies is a crucial consideration. This is because decomposers will colonize from the ends and when pieces are too short the decomposition rate is elevated. A preliminary guideline would be to have the

length 10 times longer than the mean diameter. To some extent the length problem can be avoided by using an end sealer. This may be required when short lengths have to be used because of shortage of material or extreme taper of pieces (e.g., coarse roots). Paraffin, epoxy sealer, and neoprene paint have been used in the past as physical barriers. End surfaces should be clean and dry before application of the sealer. Unless these conditions are met, most sealants will not adhere to the ends properly and the physical barrier will be incomplete.

8. Placement. Pieces can be placed upon the organic horizon, suspended, or buried in the rooting zone. While it is desirable for all these situations to be studied, we recommend that branches placed upon the organic horizon be used as the reference case for each site. If other positions are of interest, using the following methods would assure some degree of standardization. Fine wood pieces may be suspended off the soil surface using two pieces of braided nylon cord to form a ladderlike arrangement, which can then be hung from a tree. Buried fine wood should be inserted into the soil using a shovel as with buried litterbags; however, we recommend that sheets of 1 mm nylon mesh be wrapped around the pieces to aid recovery. As with litterbags, tethering all fine downed or buried wood pieces is recommended. Since many woody detritus decomposition studies may take decades to complete, it is essential that a sketch map showing the location of the pieces relative to obvious landmarks be made at the time of study initiation.
9. Sample replication. At least four sites should be sampled at each time to avoid pseudoreplication problems (Hurlbert 1984). It is recommended that if the entire branch or root is not harvested and weighed, then at least three cross sections should be taken for moisture content.
10. Sample retrieval. Tethered wood pieces should be located and uncovered before attempting retrieval. Pulling the tether line to retrieve samples may cause breakage and loss of sample. If pieces are shorter than the initial length, then the length recovered should be noted to adjust results for breakage. Clean samples of any adhering pieces of organic or mineral matter and place in a plastic bag.
11. Sample processing. In the laboratory, reclean the samples, then place into paper bags and oven dry at 55 °C until the sample weight is stable. For pieces exceeding 5 cm in diameter, cut the sample into pieces to speed drying. After oven-dry weight has been determined, chop the samples and coarse grind to 2 mm using a large Wiley or hammer mill. Grind further to pass a 40-mesh (0.417 mm) screen using a conventional Wiley mill and then store in glass or polypropylene bottles in a cool, dry environment until chemical analysis.

Calculations

Because wood ash contents are consistently low, there is usually no need to correct for soil contamination. Exceptions are coarse roots or any very decayed material that has come into contact with the mineral soil; for these types of material, corrections for ash content should follow those outlined for fine litter. Calculations used for de-

termining the composition and nutrient dynamics of woody detritus are described later.

Special Considerations

The position of the pieces with respect to the soil (suspended above, resting on, or buried within) can have a major impact on decomposition rates. Therefore, one may wish to test this effect by either burying or suspending pieces in addition to placing them on the surface of the organic horizon.

Coarse Woody Detritus Decomposition

Coarse woody detritus takes several forms, including downed and standing boles, stumps, and very large branches and coarse roots. Decomposition of large pieces (>1 m long and >10 cm diameter) of woody detritus is best studied by recording the volume of the entire piece to determine fragmentation losses and then removing disks to determine changes in density.

Materials

The materials and equipment required to conduct decomposition and nutrient studies for coarse woody detritus include the following:

1. A source of boles
2. Chainsaw
3. Hatchet to remove subsamples
4. Hammer and chisel to trim and remove subsamples
5. Calipers (0–150 mm range) to measure thicknesses of samples
6. Diameter tape to measure piece circumference
7. Tape measure or ruler to measure piece length
8. Aluminum tags to mark samples
9. Aluminum nails to attach tags to large pieces (>10 cm)
10. Plastic bags to carry samples (1–120 L depending on piece size)
11. Paper bags for drying samples (no. 2 to no. 10 depending on piece size)
12. Portable electronic scale if work is conducted at remote site
13. Electronic scales with ranges of 0–1500 g and 0–6000 g depending on piece size

Procedure

1. Sample interval. Recommendations for sample intervals are the same as for fine woody detritus.
2. Species selection. Recommendations for species selection are the same as for fine woody detritus.
3. Substrate quality descriptors. The same physical and chemical descriptors of substrate quality used for fine woody detritus should be used for coarse woody

detritus. In addition, the depth and type of any existing decay (white rot versus brown rot) should be measured. It is also useful to record the depth of the pith because this serves as a useful reference point as the piece fragments. If bark was removed during felling or transport, the total bark cover should be estimated.

4. Collection of materials. A good source of material is recently fallen trees from windstorms, or one can fell trees using a chainsaw. For coarse woody detritus allow an additional 20% to the final length to prevent sample disks from excessive drying during piece preparation.
5. Initial mass. For coarse woody detritus it is impractical to weigh samples to determine their initial mass. It is more practical to remove disks, or "cookies," from the ends of pieces to determine the density and to estimate the initial total volume of the piece. When removing disks trim off a short length (e.g., 5 cm) if the ends have been exposed to drying before cutting the sample disk. As a minimum, the end diameters and the middle diameter as well as total length should be measured for initial volume determinations of each piece (see Newton's formula below). The maximum and minimum diameter at each point should be measured with a caliper or diameter tape. Initial mass is the product of the initial volume and density of the disk.
6. Subsampling. Bark and wood should be the minimum layers that are examined on pieces exceeding 10 cm diameter because the nutrient content and decomposition rates of these materials are very different. It is also very useful to separate the sapwood from the heartwood because heartwood decay resistance is the primary basis for differences in tree species (Harmon et al. 1986). Even in species without decay-resistant heartwood, this layer decays slower than the sapwood due to the time required to colonize the inner layers. Although it is interesting to separate the inner and outer bark (these two layers are usually the fastest- and slowest-decaying layers, respectively), it is often very difficult to separate with any degree of accuracy or safety. It is therefore probably best to treat bark as one tissue and then try to separate the dynamics of the individual layers using the two-component exponential model outlined later.
7. Placement. We recommend that pieces be placed upon the organic horizon as the standard protocol for each site. Moving large pieces of woody detritus can be difficult; therefore, they may have to be left "in place." If pieces exceeding a diameter of 25 cm and a length of 2 m are to be moved, logging machinery may be required. Given that many woody detritus decomposition studies may take decades to complete, it is essential that a sketch map showing the location of the pieces relative to obvious landmarks be made at the time of study initiation.
8. Sample replication. At least three sites should be sampled at each time to avoid pseudoreplication problems (Hurlbert 1984).
9. Mass loss. After a suitable period of decomposition, determine the remaining volume, bark cover, and density of parts of the pieces. As a minimum, the end diameters and the middle diameter, as well as total length, should be measured for total volume determinations (see Newton's formula below). The maxi-

mum and minimum diameter at each point should be measured with a caliper or diameter tape. This current volume should be compared with the estimated original volume to see if a correction for fragmentation losses is required. Total bark cover should also be estimated, using a frame of known size to help determine the total area missing or remaining. To determine the density, moisture, and nutrient content of a piece, a minimum of three disks should be removed per piece, and these should be systematically spaced along the length.

Various methods are used to remove subsamples of decomposing bark and wood for density, moisture, and nutrient determination. These include mapping out and subsampling zones with different appearance (Sollins et al. 1987; Harmon et al. 1987), systematically cutting the disk into pieces (Harmon 1992), removing "typical" subsections, or removing entire tissue layers (e.g., bark). Unless one is interested in studying the internal heterogeneity, we suggest the latter approach. If fragmentation of layers has not occurred, then record the diameter with and without a layer, as well as the longitudinal thickness (along the long axis of the piece) of each layer in a disk. Use a hammer and chisel to separate the layers. The total fresh weight of each layer can then be determined and a subsample used to determine the moisture and nutrient content of each layer. The volume of each layer is calculated as for a cylinder,

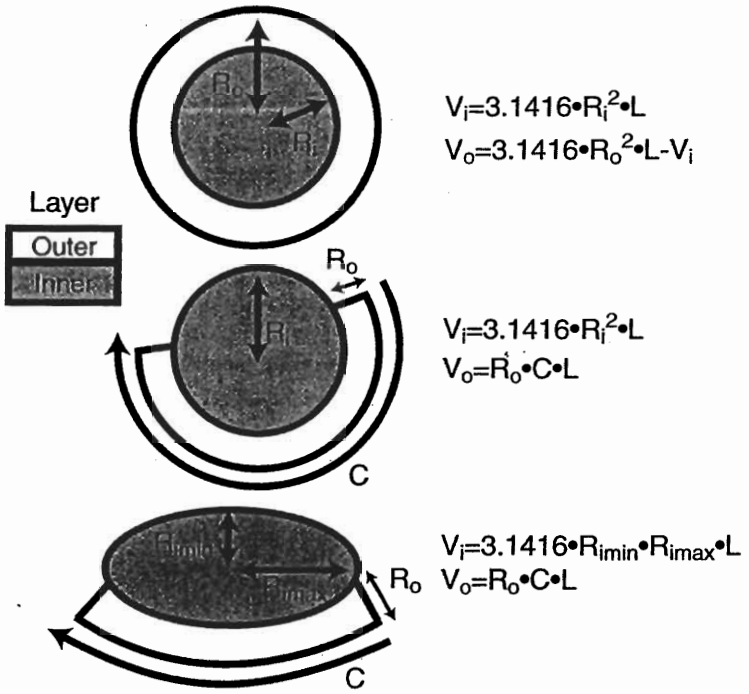


Figure 11.1. Measurements to be taken and appropriate formulas to determine volume of layers within a cross section removed from a piece of large woody detritus. *R* is the radial dimension, and *C* is the length along the circumference. *L* is the longitudinal dimension and is not shown on the cross-section drawings. The subscripts indicate whether the dimension is from the inner (*i*) or outer layer (*o*) or the minimum (*min*) or maximum (*max*) axis.

with the volume of any layer occurring inside it deducted (Fig. 11.1). If fragmentation of a layer has occurred, then record the radial thickness and circumferential length of the layer as well as its longitudinal thickness. The volume of this layer can be computed as a rectangular form. Compute the volume of the remaining unfragmented layers as described earlier for unfragmented disks. Extremely decomposed pieces often have elliptical forms, and it is also difficult to remove intact disks from them. In this case it is best to cut the disk free and then carefully excavate it from the piece. One can then record the maximum and minimum diameters of the disk from the parts that were not removed. The area of the elliptical disk can be computed using the equation for an ellipse. The longitudinal thickness of elliptical pieces can be determined from the pieces of the cross section that are removed. Separation of layers, weight determination, and subsampling for moisture and nutrient contents for these last two cases are the same as for unfragmented disks. Subsamples should be chopped into smaller pieces and placed in paper bags to be oven dried at 55 °C until the weight is stable. The oven-dry weight of the total disk can be computed by multiplying the ratio of oven-dry weight to fresh weight of the subsample by the total fresh weight of the layer. Subsamples for a given layer and pieces may be pooled, coarse ground, fine ground, and stored as for fine wood samples.

Calculations

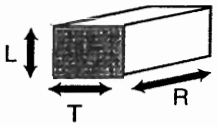
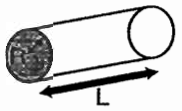
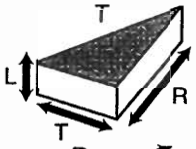
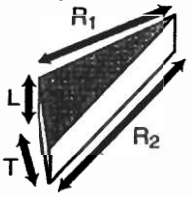
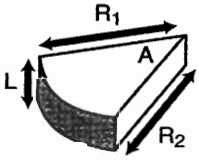
Because wood ash contents are consistently low, there is usually no need to correct for soil contamination except in locations where insects transport soil into downed wood. Calculations used for determining the composition and nutrient dynamics of woody detritus are described later. Use of the two-component exponential equation is highly recommended when tissue layers with highly different properties (e.g., outer and inner bark) are not physically separated. Density calculations should be based on oven-dry mass divided by green or fresh volume because wood below 30% moisture content (the fiber saturation point) will shrink. Equations for calculating the volume of samples are presented in Fig. 11.2.

Special Considerations

The method proposed to estimate the volume of samples is likely to overestimate the volume of bark for species with rough surfaces. If this is a concern, then displacement measurements should be used to determine volume. If water displacement is used, then separate samples should be used to determine nutrient concentrations.

Standard Substrate Decomposition

The recommended standard substrates to be used in conjunction with fine litter or woody detritus decomposition experiments are cellulose filter paper and hardwood dowels. The advantage of using these materials is that they are more likely to be uni-

Form	Equation[1]	
Rectangular	V= L T R	
Cylinder	V=3.142 L R^2	
Triangular isoceles	V=0.5 L T R	
Triangular general	V=Sqrt $[(S)(S-R_1)(S-R_2)(S-T)]L$ $S=(R_1+R_2+T)/2$	
Sector of Circle	V=3.146 L R_2 (A/360) R= $(R_1+R_2)/2$	

[1]V is the volume, L is the longitudinal, T is the tangential, and R is the radial dimension, respectively. In the case of a cylinder R is the radius. In the case of a sector of a circle, A is the angle (degrees) formed by the two radii (R_1 and R_2).

Figure 11.2. Commonly used formulas to calculate the volume of samples used for density.

form and they are very sensitive to nutrient availability. Both characteristics make them ideal for directly comparing the effects of the environment among studies and sites (Binkley 1984; O'Lear et al. 1996).

Materials

The materials needed to construct, place, and retrieve standard substrates include the following:

1. Cellulose filter paper.
2. Litterbags (see earlier for construction guidelines)
3. Nylon thread or Monel staples to seal the litterbags
4. Tags, either aluminum or plastic
5. Flagging to mark location

6. Hardwood dowels, 6 mm diameter; 60 or 120 cm long
7. Dowel sleeves (see later for construction guidelines)
8. Steel rebar, 6 mm diameter, 45 cm long, and hammer to make pilot hole for dowel
9. Heavy nylon monofilament or braided nylon line to tether litterbags
10. Plastic bags to transport and store retrieved litterbags and dowels
11. High-quality paper bags to dry litter
12. Drying oven with a 50–55 °C range
13. Data forms to record the time of recovery, fresh weight, oven-dry weight, and any peculiarities of the samples

Required materials and construction of litterbags for incubating cellulose filter paper are the same as for those containing natural fine litters. For hardwood dowels, some modification is required. If the dowels are to be placed belowground, they should be encased in a sleeve of 1 mm nylon mesh. This can be constructed by sewing a narrow strip of nylon mesh (4 cm wide and 30 cm long) into a sleeve that can be slipped over the portion that is placed below ground. This greatly aids in the recovery of the decomposed dowels from soil.

For dowel studies we recommend using a hardwood species that does not have a decay-resistant heartwood because this reduces variation both within and between species. Species commonly available with this characteristic include ramin (*Gonystylus bancanus*), birch (*Betula* spp.), and basswood (*Tilia* spp.).

Procedure

1. Cellulose standard substrates. Procedures for filling litterbags with cellulose filter papers are the same as for litterbags using natural litters. We recommend using 5–10 g of paper. Placement should be similar to that of the natural litter that is being placed. In addition, it may be of interest to place filter paper filled bags at several depths within the soil. Recovery and treatment of the decomposed material also follow the procedures for fine litter (see earlier). Because the nitrogen concentration of filter paper varies, it is essential this parameter be reported when results are presented.
2. Dowel standard substrate. Procedures for the hardwood dowels are similar to those for small woody detritus pieces. Use 60 cm lengths of 6 mm diameter dowel. Our recommended protocol is to place 30 cm of the dowel belowground and 30 cm aboveground so that these two environments can be compared. UV-resistant cable ties should be used to attach tags to the aboveground portion of the dowels. For the belowground portions attach a tag (with the same number as that on the upper portion) to the nylon mesh sleeve that will eventually encase it. Weigh the entire dowel after taring out the weight of the cable tie and tag attached to the upper portion. As with fine litter, periodically save subsamples to determine the oven-dry weight to air-dry weight conversion factor and to have materials for initial chemical analysis. After the dowel is weighed, slip the nylon mesh sleeve over the portion that is to be placed belowground.

3. Dowel placement. Dowel placement will largely depend on the design of other experiments being conducted. Once a location is selected, we recommend driving a 6 mm diameter by 45 cm long piece of steel rebar into the soil to form a pilot hole in which to place the dowel. Mark the 30 cm depth on the rebar so that the hole is the correct depth. In very rocky soils, it may be necessary to search for a "rock-free" zone or to place the dowels at a shallower depth. Slide the dowel into the pilot hole and note the length of the dowel remaining aboveground.
4. Dowel retrieval and processing. Retrieving the dowel involves finding the aboveground portion (it may no longer be attached to the belowground part) and placing it in a plastic bag. For the belowground portion, locate the tag attached to the nylon sleeve, excavate the dowel using a shovel, and place it in a plastic bag. As the dowel parts are recovered it is important to record the lengths of the above- and belowground parts that are found, as well as noting any obvious insect damage. In the laboratory, brush off any soil still adhering to the dowel with a moist paper towel and clip the above- and belowground portions into short (2–5 cm) sections so they will fit in a small paper bag and dry faster. Dry at 55 °C until the mass is stable (5–7 days) and record the dry weight. To grind the dowel samples in a standard Wiley mill, it may be necessary to first coarse grind to a 2–3 mm particle size by using a larger mill. Store ground samples in closed glass or polypropylene containers in a cool, dry environment until analysis can be conducted.

Calculations

Results for standard substrates should be reported in ash-free values. Calculations of mass loss and adjustments for soil contamination should be the same as those for fine litter. To calculate the initial oven-dry weight of the above- versus belowground portions of dowels, assume that the density is uniform:

$$IODW_{position} = IODW_{total} \times Length_{position}/Length_{total}$$

where

$IODW_{position}$ = the initial oven-dry mass of the position (above- or belowground)
$IODW_{total}$ = the total initial oven-dry mass
$Length_{position}$ = the portion of the dowel in a position
$Length_{total}$ = the total length of the dowel

Special Considerations

There is likely to be some spread of decomposers from the belowground portion of the dowel into the aerial portions. Using separate dowels for above- and belowground measurements will eliminate this effect. One may also suspend dowels in the air to prevent incorporation into the organic horizon. Further subdivision of the dowels beyond the above- and belowground segments recommended here is also possible.

Organic Horizon Stores

The organic horizons to be sampled may be composed of many forms of plant litter. To avoid double counting, one should not include any wood pieces that are greater than 1 cm in diameter and recognizable as branches or boles. Measurements for these materials are described later. Organic horizons should include any thoroughly decomposed wood (usually red-brown in color) that is located in the organic horizon. Although this is often discarded as a nonorganic horizon, it can constitute a considerable fraction of some organic horizons, especially in conifer forests (McFee and Stone 1966; Youngberg 1966; Harvey et al. 1979; Harvey et al. 1981; Little and Ohmann 1988). This material is important to include because it is the wood analog to the humus or O_2 layer in a forest floor and can have high nitrogen availability (Sollins et al. 1987).

The methodology proposed, sampling in 25 cm × 25 cm quadrats, is suitable for most situations where organic horizons are continuous. In situations where organic horizons are sparse or interspersed with rock outcrops, bare soil, logs, or other objects that cover more than 5% of the surface, we recommend a stratified sampling, with line transects being used to determine the area covered in organic horizons versus the other surfaces. Organic horizons that are sampled can then be adjusted to represent the overall area.

A final sampling consideration is the time of year to sample. In ecosystems with distinct pulses of litter inputs, seasonal variation in organic horizon stores can vary by 20–30% (Loomis 1975). This variation can be almost as large as that observed over succession (Federer 1984); it is therefore important to note the season of sampling relative to the peak in litter inputs. Ideally sampling should be conducted before and just after the peak litter inputs so that the annual range in stores would be available for comparative purposes.

Materials

The materials required to sample organic horizons are

1. Wooden or steel sampling template, 25 cm × 25 cm recommended
2. Serrated knife to cut organic horizons
3. Small pruning saw to cut buried branches and coarse roots
4. Pruning shears to cut buried branches and coarse roots
5. Small file to sharpen bottom edge of frame
6. Plastic or plastic-lined paper bags to store samples
7. 30–50 m tape to locate sample points and determine cover of nonorganic surfaces
8. Sorting tray larger than frame to field process sample
9. Random number table

The sampling template can be made out of wood or metal. If a metal template is to be used we recommend it be fashioned as an open frame constructed from stainless steel and welded together. Handles can also be welded on the frame to help push it into the organic horizon. The bottom edge of the metal frame can be sharpened

with a file to help it cut through the organic layers. Paper bags for storing samples should be avoided unless they are lined with plastic, since moisture from the samples will weaken even the thickest paper bags.

Procedure

1. Site characterization. Once an ecosystem has been located for sampling, one must decide if the cover of surfaces other than the organic horizon exceeds 5%. If the cover is less than 5%, then proceed to sample the organic horizon as outlined later. If the cover of nonorganic horizon surfaces exceeds 5%, then use line transects to determine the cover of these surfaces. A transect length of at least 100 m should be used to record the length covered by surface rocks and outcroppings, exposed mineral soil, tree roots, logs, stumps, or other surfaces that will be sampled by other means. Ideally the transect or grid used to sample organic horizon cover can also be used for the location of samples. If the ecosystem occurs on sloping ground, it is important to note the average slope steepness because results should be reported on a horizontal and not a slope area basis.
2. Plot placement and replication. Sample plots for organic horizons can be placed either systematically or at randomly spaced locations along the tape measure. The number of samples adequate for an ecosystem will vary. The use of two to three samples (e.g., Metz 1954; Youngberg 1966; Loomis 1975) is strongly discouraged. As a starting point, we recommend 20–50 samples to provide a standard error within 10% of the mean (McFee and Stone 1965; Wallace and Freedman 1986). It is also useful to plot a running mean of samples to determine when additional samples change the mean less than 5%.
3. Sample removal. Once the samples are located along the transect or grid, place the sample template parallel to the surface and press it into the organic horizon until firm resistance is felt. Use a knife to cut the organic layer and pruning shears or saw to cut any roots or buried branches that prevent cutting through to the mineral soil.

   Remove the template, and remove the organic horizon and any mineral soil adhering to the bottom. A spatula can often be used to lift the intact sample off the underlying horizons. Place the sample in a metal sorting tray as intact as possible and remove any adhering mineral soil. It is important to consistently remove the mineral soil from the organic horizon. Remove any branches greater than 1 cm in diameter from the sample and place the remaining sample in a plastic or lined paper bag that is sealed and clearly labeled with the date, location, sample number, and any other critical information. If red-brown, thoroughly decayed wood is found in the sample, separate this from the rest of the material and bag it separately. Further separation of other organic layers is optional (e.g., O1 versus O2), but given the different systems used for each ecosystem, it is unlikely these values could be directly compared outside a given region. The separation of decayed wood is quite important because this material has generally not been measured and is derived from a source different than the rest of the organic horizon.

4. Sample processing. In the laboratory, the samples should be removed from the plastic bags, placed in heavy paper bags or trays, and oven dried at 55 °C until the weight is stable. After determining the dry weight, samples may be pooled to determine chemical properties, since there is a good correlation between pooled samples and the mean of individual samples for most properties (Carter and Lowe 1986). However, if one is interested in the internal variation within a plot or experiment, then we would recommend against sample pooling for determining chemical properties. Samples used for chemical properties should be passed through a screen and homogenized. Subsamples of the material should be ground to 40-mesh sieve and stored in glass or polypropylene containers in a dry, cool location until ash and nutrient contents can be determined (see Chapter 8, this volume).

Calculations

Results should be expressed as ash-free mass using the methods described for fine litter decomposition experiments. For ecosystems where organic horizons cover less than 95% of the surface, the total store in organic horizons should be decreased to represent the average surface:

$$Mass_{corrected} = Mass_{OH} \times Area_{OH}$$

where

$Mass_{correctin}$ = the organic horizon mass corrected for other surfaces
$Mass_{OH}$ = the mass of the surfaces covered by organic horizons
$Area_{OH}$ = the fraction of the ecosystem covered by organic horizons

If the ecosystem occurs on a slope exceeding 10°, then a correction should be made to report results on a horizontal area basis. The equation for this correction is:

$$Mass_{slope\ corr} = \text{cosine}\ (slope) \times Mass_{slope}$$

where

$Mass_{slope\ corr}$ = the slope corrected mass
$slope$ = slope angle in degrees
$Mass_{slope}$ = the mass of organic matter based on slope distance

Special Considerations

Separation of organic horizons from the upper mineral soil is problematic for many soils. Distinctions between organic and mineral horizons are clearer in mor-type layers, but are quite gradual in mull-type layers. In the latter case, close coordination of sampling of the organic and upper mineral horizons is crucial to avoid double counting of stores. Ash content of organic horizons in mull soils is likely to be highly variable; therefore, determining the ash content of each sample is recommended in this case.

Fine Woody Detritus Stores

The forms of fine woody detritus that should be sampled include downed and suspended fine wood (<10 cm diameter and <1 m long), and dead coarse roots. For meaningful comparisons it is extremely important to include all forms of woody detritus in inventories and to report them in the same units.

The recommended protocol is to define a large plot (hopefully the same area in which ongoing experiments or live biomass measurements are being conducted). Use 10–20 1 m × 1 m subplots to estimate the mass of downed fine wood, and use allometric relationships to estimate the stores of dead coarse roots and fine woody detritus attached to standing dead trees. Fine downed woody detritus can be directly harvested, weighed in the field, and subsampled for moisture and nutrient content.

Materials

The materials needed to measure fine woody detritus stores are

1. Diameter tape for measuring diameters of standing dead trees and stumps
2. 30 or 50 m tape for defining plot boundaries
3. Compass to help lay out plot boundaries
4. Flagging to mark boundaries of large plot
5. 1 m × 1 m sample frame to define downed fine woody detritus plot
6. Pruning saw and/or clippers to cut fine downed woody detritus
7. Portable scale, electronic version with accuracy to 1 g preferred
8. Burlap or other large cloth bags to hold fine wood samples
9. Tray to hold fine wood samples while weighing
10. 1–4 L plastic bags to hold fine wood moisture samples

Procedure

1. Sample selection and number. To be most useful, fine woody detritus should be measured in plots or stands that have ongoing experiments or inventories of living biomass and other detrital pools. Because the distribution of fine downed wood is highly variable, we recommend that at least 10–20 subplots be used for each stand sampled (Harmon and Sexton 1996), since this results in estimates with a standard error within 30% and 20% of the mean, respectively (Harmon and Sexton 1996). Alternatively, a running mean may be plotted for a subset of samples to assure adequate replication (i.e., addition or subtraction of a sample does not change the overall mean more than 5%).
2. Downed fine woody detritus. Downed fine wood should be estimated in 1m × 1 m fixed-area subplots. The entire subplot, including the organic horizon, should be searched. Woody material that is <1 cm diameter or decayed to the point its source is not recognizable should not be gathered because such material is considered part of the organic horizon. Once all the fine woody material is harvested, weigh using a portable electronic scale. Spring scales should be avoided due to their general lack of precision. Subsamples of this wood (100–200 g) are then taken and weighed in the field, oven dried at 55 °C, and weighed to determine the moisture content. The total field weight

is then adjusted using the estimated field moisture content. An alternative is to remove the entire sample to be weighed and dry it in the laboratory; given the volume of material this entails, however, subsampling may be preferred.

3. Suspended fine woody debris. It is extremely difficult to estimate suspended fine wood directly unless it is close to the ground, where it should be included in the 1 m × 1 m plots used for downed fine wood. We recommend that an indirect estimate be used, based on the inventory of standing dead tree mass. For standing dead trees that are not broken, one should estimate the volume of branches from allometric equations. For boles that have broken, this volume should be pro rated according to snag height so that only snags with the entire length have the entire branch volume and those that have broken off below the crown do not have any branch volume. The mass of suspended fine wood should then be estimated from the branch volume by multiplying the branch bulk density for the appropriate snag decay class. Unfortunately, there are few estimates of branch density as a function of snag decay class. Lacking such data, assume a branch density.
4. Dead coarse roots. We know of no one who has tried to directly inventory dead coarse roots by excavation, but given the potential mass of material, some estimate should be made. One possible indirect method is to use allometric relationships based on tree diameter to predict the volume of dead roots for each dead tree in the fixed-area plot used to sample coarse woody detritus. Rather than use the diameter at breast height, which would not be available for stumps or many logs, the diameter at the piece base should be measured for this purpose. Equations exist to convert basal diameter to diameter at breast height for many species (Harmon and Sexton 1996). Predict dead coarse root volume for each dead tree inventoried and then use the bulk density of dead roots to estimate the mass. As with suspended fine wood, until bulk density data for decomposing coarse roots become generally available, it may be necessary to assume a value.

Calculations

Corrections for stores measured on plots with a slope greater than 10° are the same as those for organic horizons. Because woody detritus generally has a very low ash content (i.e., <2%), correcting for soil contamination is less of a concern than for organic horizons.

Special Considerations

Other methods are more suited to larger-scale surveys. Planar transects are particularly useful in this context, although other methods will have to be used to estimate suspended fine wood and dead coarse roots.

Coarse Woody Detritus Stores

The forms of coarse woody detritus that should be sampled include stumps (specifically meaning the lower part of trees that were cut by a saw), downed coarse wood

(hereafter called logs, >10 cm diameter at the large end and >1 m long), and standing dead trees (including everything from freshly killed trees to extremely decayed, short vertical pieces not cut by saw). For meaningful comparisons it is extremely important to include all forms of woody detritus in inventories and to report them in the same units. Past synthesis efforts have been severely hampered because these two problems have repeatedly not been considered in the primary literature (Harmon et al. 1986; Harmon 1993). For example, reporting standing dead trees as numbers per area and downed wood as volume per area (as is common) makes it impossible to total stores.

The recommended protocol is to define a large plot (preferably the same area in which ongoing experiments or live biomass measurements are being conducted) and to measure the dimensions of all large pieces of woody detritus on the entire plot. The volumes of large woody detritus estimated from the dimensional data can be converted to mass and nutrient stores using decay class–specific bulk density and nutrient concentration data.

Materials

The materials needed to measure coarse woody detritus stores are

1. 1 m caliper for measuring diameters of downed maerial
2. Diameter tape for measuring diameters of standing dead trees
3. 30 or 50 m tape for defining plot boundaries and measuring pieces' lengths
4. Clinometer to determine standing dead tree heights
5. Compass to lay out plot boundaries
6. Flagging to mark boundaries of large plot
7. Sample forms, clipboards, etc., for recording data
8. In addition to these materials, it is also essential that investigators check into the availability of decay classifications and bulk density values for their local species and situations (see Harmon and Sexton 1996 for some compiled values). It is entirely unacceptable to use unrelated genera (e.g., *Pseudotsuga*) to convert volume to mass and nutrient stores; unfortunately, this has occurred in the past. If suitable conversion factors do not exist, then a serious effort needs to be made to create them.

Procedure

1. Plot selection and size. To be most useful, woody detritus should be measured in plots or stands that have ongoing experiments or inventories of living biomass and other detrital pools. This gives a more complete inventory of the ecosystem but also allows coupling of process rates (e.g., mortality) to these "static" measurements. For large pieces of woody detritus, plot size is a crucial consideration. The size of the coarse woody detritus plots may correspond to that of preexisting tree plots. If new plots are being established, a cumulative area of at least 0.1 ha to represent a normally stocked stand is recommended. Even with this plot size, at least 10 replicates may be required to have the standard error range within 10% of the mean (Harmon and Sexton 1996).

2. Dimension measurements. Large or coarse woody detritus assumes at least four forms: standing dead trees (also called snags), stumps, logs, and blobs. The last refers to the piles of decomposed bark and wood that accumulate around the bases of large snags. The variables recorded for each log inventoried include diameters at both ends and at the midpoint, length, species, position, and decay class, and whether the piece is hollow or solid. In many forests it is very important to subtract out the volume associated with hollows by noting the diameter and length of the hollow as well as the exterior diameter. The variables required for all other forms of large woody detritus are similar to those used for logs, with the exception of diameter. For snags, the diameter at breast height is recorded for intact boles, and the diameters at the base and top for boles that have broken. The base and top diameters can also be recorded for stumps. Finally, the diameter at the base is the only dimension required for blobs.
3. Diameters are best measured using 100 cm calipers because it is often impossible to wrap a tape around logs and parallax errors are large if a meter stick is used. When pieces are elliptical, record the maximum and minimum diameters and convert to a round-equivalent diameter using a modified version of the formula for the area of an ellipse. The top diameter of tall snags can usually be accurately measured by simply finding the top. If the top cannot be located, a visual estimate will usually suffice as long as one calibrates one's eye.
4. The length of logs can be measured with a tape or, if available, a sonic tape measure. The height of snags is often difficult to measure or estimate. If the snag is not broken, estimate the snag volume or height from the breast-height diameter by using allometric relationships developed for living trees. If a snag is not intact, then estimate the length or height. For snags less than 4 m, use a 100 cm caliper or meter stick to estimate height; for taller snags, a clinometer and tape can be used.
5. Volume to mass conversion. Regardless of the dimensions measured, these data must first be converted to volume and then to mass to estimate mass and nutrient stores. To convert from volume to mass or nutrient stores, use the density and/or nutrient content of wood and bark in various stages of decay. The latter values can be taken from the literature, although there exists potential for error by not using site-specific values (especially for nutrient stores). It is preferable that decay class conversion factors be site-specific, although this need not include every forest for which dimensional data are gathered. To establish an objective decay class system, it is necessary to correlate the external characteristics to variables of interest such as density, bark cover, and nutrient content. Samples are then removed from three to five logs of each decay class to determine the mean bulk density and nutrient concentration (see the section "Coarse Woody Detritus Decomposition," above, for sampling methods).
6. It is crucial to report the characteristics used to separate decay classes for data to be comparable. Unspecified modifications of another decay class system are not sufficient descriptions. Physical characteristics that have proven use-

ful in the past to distinguish decay classes include presence of leaves, twigs, branches, bark cover on branches and boles, sloughing of wood, collapsing and spreading of log (indicating the transition from round to elliptical form), degree of soil contact, friability or crushability of wood, color of wood, and whether the branch stubs can be moved. Biological indicators such as moss cover, fungal fruiting bodies, or presence of insect galleries seem to be of very little value in separating decay classes because they vary widely even within a limited area. In areas with high species diversity, it will probably be impossible to have decay classes measured for each species. This problem can be addressed by defining larger functional classes, such as decay-resistant and non-decay-resistant species (Harmon et al. 1995).

Calculations

Corrections for stores measured on plots with a slope greater than 10° are the same as those for organic horizons. As woody detritus generally has a very low ash content (i.e., <2%), correcting for soil contamination is less of a concern than for organic horizons.

To convert the maximum and minimum diameters of elliptical pieces to a round diameter equivalent, use a modified version of the formula for the area of an ellipse:

$$A = D_{max} \times D_{min}$$

and backtransform to diameter using a modified version of the area of a circle:

$$D_{round} = \sqrt{A}$$

where

D_{max}, D_{min}, and D_{round} are the maximum, minimum, and round equivalent diameters, respectively

The volume of large woody debris pieces can be calculated by several formulas, depending on the number of diameter measurements taken. For logs in which diameters were measured at three points use Newton's formula:

$$V = L \times [A_b + (4 \times A_m) + A_t]/6$$

where

V = the volume
L = the length
A_b, A_m, and A_t = the areas of the base, middle, and top, respectively

For logs, standing dead trees, or stumps that have two diameter measurements, use the formula for a frustum of a cone to estimate volume:

$$V = L \times [A_b + (A_b A_t)^{0.5} + A_t]/3$$

where

V = the volume
L = the length
A_b and A_t = the areas of the base and top, respectively

For blobs, which only have the basal diameter measured, use a modified version of the formula for a paraboloid to estimate volume:

$$V = L \times (A_b/2)$$

where

V = the volume
L = the length
A_b = the area of the base

Special Considerations

Other methods are more suited to larger-scale surveys. Planar transects are particularly useful in this context, although other methods will have to be used to estimate stumps and standing dead trees. It is essential that decay classes similar to those used in fixed-area plots be used, since the original sound-versus-rotten classification suggested by Brown (1974) is too crude. Methods for other forms of woody detritus, which might work in a large-scale survey context, would include variable-radius plots (Grosenbaugh 1958; Harmon and Sexton 1996) and point-centered quarter sampling (Cottam and Curtis 1956; Mueller-Dombois and Ellenberg 1974). These alternative methods, however, have yet to be tested.

Calculation of Decomposition and Nutrient Mineralization Rates

Time-series data, such as that generated from litterbag studies, can be presented as the percentage of initial mass remaining over time. "Decomposition curves" can also be mathematically described. Once weights have been corrected for mineral soil contamination (see the "Fine Litter Decomposition" section, below), the percent mass remaining can be calculated. Initial air-dry weights should be converted to equivalent oven-dry weights before doing this. Percent mass remaining from individual litterbags can be averaged, and mean percent mass remaining over time can be plotted, by treatment or litter type, and used to calculate decomposition rate constants.

There are several available models to which mass loss data can be fit (Olson 1963; Minderman 1968; Wieder and Lang 1982; Andren and Paustian 1987). The simplest of these is the single negative exponential model (Jenny et al. 1949; Olson 1963) of the form:

$$X_t/X_0 = e^{-kt}$$

where

X_t/X_0 = proportion of litter mass remaining at time t
t = time elapsed, expressed as years or days (see discussion)
e = the base of the natural logarithms
k = the decomposition rate constant

This model is attractive because it produces a single decomposition rate constant (k value), which can be used to compare data from different treatments, species, or studies. Thus, we recommend the calculation of decomposition rate constants using this model when possible. A major disadvantage is that it does not accurately describe litter decomposition kinetics where relative decay rates vary over time, as is the case when there is a rapid loss or an extended lag phase early in decomposition.

The single negative exponential model can be fit to the data by least-squares linear regression of the natural logarithm of mean percent mass remaining over time. To calculate annual decomposition rate constants, time in the field should be expressed as a fraction of 1 year (i.e., 182 days = 0.5 years). For litter types that decompose much faster, such as green crop residues, daily decomposition rates may be more appropriate. Least-squares regression will give values for slope (k), intercept (predicted % mass remaining at t = 0), and coefficients of determination (r^2). Values of k indicate the rate of mass loss; greater k values indicate faster mass loss rates.

Intercept values are often not reported, although they can provide insight into both the appropriateness of the single exponential model and the kinetics of the decomposition process (Witkamp and Olson 1963; Harmon et al. 1990, 1995). Intercepts that are significantly below 100% at t = 0 indicate a more rapid loss of material early in decomposition than would be predicted by the single negative exponential model (Fig. 11.3). Conversely, intercepts significantly above 100% indicate an extended lag phase early in decomposition, which may be due to climate or may indicate a colonization or conditioning phase. We strongly suggest that the mass remaining at each sample time be reported in tabular form and/or included in graphic presentations of the modeled decomposition curves generated, thus allowing reanalysis in future syntheses.

In cases where the single negative exponential model does not fit the data well, a multiple-component exponential model may be appropriate (Wieder and Lang 1982). This model assumes that the litter can be partitioned into two fractions, one labile and one more recalcitrant. This model may be more appropriate for litter types that exhibit a rapid mass loss phase followed by slower decomposition. Another model is the single negative exponential with asymptote, in which mass loss declines to zero and a fixed proportion of recalcitrant litter remains. Although this is not realistic over longer time scales, it may be appropriate for estimating the amount of "stable" organic matter produced as a product of litter decomposition.

In addition to mass loss, changes in litter nutrient concentrations and patterns and amounts of net nutrient accumulation and release should be calculated if nutrient analyses are available. Patterns of net accumulation and/or release of nutrients are typically more complex than patterns of mass loss, since nutrients can accumulate in the litter, microbes, and microbial by-products as decomposition proceeds. The

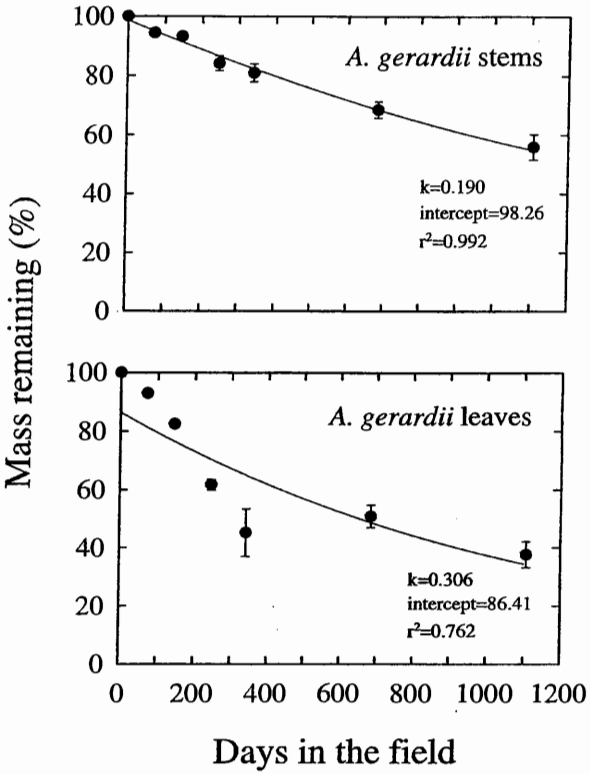


Figure 11.3. Illustration of the fit of a single exponential decomposition model to litter decomposition data. Top: Pattern of mass loss for stems of the C_4 grass big blue stem (*Andropogon gerardii*) decomposing at Konza Prairie. Solid symbols represent the mean percentage of initial mass remaining after 72, 146, 247, 342, 685, and 1107 days in the field. The solid line is the decomposition curve generated by fitting the field data to a single negative exponential decomposition model. Also presented are the annual decomposition rate constant (k), the y intercept, and the coefficient of determination (r^2). Bottom: The same data are presented for leaves of *A. gerardii* decomposing at the Konza Prairie. Note the lower coefficient of determination and lower y-intercept value than in the case for stem decomposition. This is due to a more rapid loss of material early in decomposition and a slower loss of mass later in decomposition than would be predicted by the single negative exponential model. This suggests a two-component model might be more appropriate to describe leaf decomposition.

processes controlling these three mechanisms differ, but they are inseparable. We recommend the terms *net release* and *net accumulation* in place of *net mineralization* and *net immobilization,* respectively, since it is not possible to distinguish actual conversion of organic to inorganic forms of nutrients (mineralization) or microbial uptake (immobilization) with these methods (Berg 1988). In fact, a considerable proportion of the nutrients released from decomposing litter may be in

organic form (Yavitt and Fahey 1986; Setala et al. 1990; Qualls et al. 1991), and physical processes as well as microbial uptake may retain nutrients in litter.

It also is important to recognize that changes in nutrient concentration and net accumulation/release are not synonymous. That is, net accumulation/release is a function of both mass loss and changes in the nutrient concentration of the residual litter. Changes in nutrient concentration over time may be presented graphically. However, additional information can be acquired by examining changes in nutrient concentration in relation to mass loss (Aber and Melillo 1980). Net accumulation/release can be calculated as the product of proportion mass remaining at time t and the nutrient concentration in the residual litter at t, divided by the initial nutrient concentration in that litter type, and then plotted as a function of time. A discussion of the behaviors of various nutrients in decomposing litter is beyond the scope of this chapter. However, many references describe pattens of nutrient accumulation and release in decomposing leaf (Gosz et al. 1973; Berg and Staaf 1981; Blair 1988a, 1988b) and woody litter (Harmon et al. 1986; Sollins et al. 1987; Arthur and Fahey 1990; Harmon and Chen 1992).

Conclusions

Plant litter decomposition is a key ecosystem process that plays major roles in determining carbon and nutrient accumulation in soils, as well as in regulating the rate and timing of nutrient release to plant roots and soil organisms. In addition to understanding the dynamics of plant litter, it is essential to quantify the stores or standing stocks of these pools. Our ability to understand and quantitatively model these processes and pools will be much improved if researchers use comparable methods. This chapter has examined commonly used methods and presented standard protocols to determine the decomposition dynamics and stores for most forms of dead plant matter. These include (1) the litterbag method for determining the rate at which fine litter decomposes and accumulates or releases nutrients; (2) time-series experiments to study the decomposition and nutrient dynamics of woody detritus above- and belowground; (3) using cellulose filter paper and hardwood dowels as two standard substrates; (4) determining organic horizon stores by harvesting in 25- by 25 cm quadrats; (5) determining fine woody detritus stores ($<$10 cm diameter and $<$1 m long) by harvesting in 1- by 1-m quadrats; and (5) determining coarse woody detritus stores ($>$10 cm diameter and $>$1 m long) by recording piece dimensions in large plots and converting volume to mass or nutrient stores using species-specific and decay class–specific bulk densities and nutrient concentrations.

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